



Mojokerto revisited: Evidence for an intermediate pattern of brain growth in *Homo erectus*



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ABSTRACT

Brain development in *Homo erectus* is a subject of great interest, and the infant calvaria from Mojokerto, Indonesia, has featured prominently in these debates. Some researchers have suggested that the pattern of brain development in *H. erectus* resembled that of non-human apes, while others argue for a more human-like growth pattern. In this study, we retested hypotheses regarding brain ontogeny in *H. erectus* using new methods (resampling), and data from additional *H. erectus* crania. Our results reveal that humans achieve 62% ($\pm 10\%$) and chimpanzees 80% ($\pm 9\%$) of their adult endocranial volume by 0.5–1.5 years of age. Using brain mass data, humans achieve on average 65% and chimpanzees 81% of adult size by 0.5–1.5 years. When compared with adult *H. erectus* crania ($n = 9$) from Indonesian sites greater than 1.2 million years old, Mojokerto had reached $\sim 70\%$ of its adult cranial capacity. Mojokerto thus falls almost directly between the average growth in humans and chimpanzees, and well within the range of both. We therefore suggest that brain development in *H. erectus* cannot be dichotomized as either ape-like or human-like; it was *H. erectus*-like. These data indicate that *H. erectus* may have had a unique developmental pattern that should be considered as an important step along the continuum of brain ontogeny between apes and humans.

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Introduction

The Mojokerto specimen (also known as Perring 1) is a nearly complete child's calvaria discovered in 1936 on Java, Indonesia. This skull is the only well-preserved example of a *Homo erectus* infant, providing unique information about *H. erectus* development, with implications for the evolution of human childhood. The dating of this skull has been a point of contention due to variable reporting of the location of its discovery (Huffman, 2001; Huffman et al., 2006). Some have suggested that the Mojokerto skull may be ~ 1.81 million years old (Ma) and therefore the earliest evidence for a hominin migration out of Africa (Swisher et al., 1994). A re-dating of pumice deposits near the presumed region of discovery suggested to Moorwood et al. (2003) that the cranium is < 1.49 Ma. The relocation study carried out by Huffman et al. (2006) presents a thorough evaluation of the location at which the Mojokerto skull was found and supports a younger date since the fossil was found 20 m above the 1.81 Ma horizon. Though further analysis may continue to adjust the date of the Mojokerto skull (Huffman et al., 2006), we consider it here to be between 1.2 and 1.8 Ma, nearly

contemporaneous with fossils from the Lower Bapang (Kabuh) formation of the Sangiran Dome on Java (Larick et al., 2001).

In addition to the geological age, the chronological age of Mojokerto has been controversial in part because no teeth are preserved. Several different ages at death have been proposed, ranging from 0 to 8 years. These include the following estimates: 2–5 years (von Koenigswald, 1936); 18 months (Weidenreich, 1940); 4–6 years (Antón, 1997); and most recently 0.5–1.5 years (Coqueugniot et al., 2004). Coqueugniot et al. (2004) used CT scans of the calvaria to determine that the anterior fontanelle had not yet closed, suggesting an age at death of between 0.5 and 1.5 years. Here, we assume that this age estimate of 0.5–1.5 years for Mojokerto is correct, though we are aware that this is subject to change with future studies of this calvaria, and discoveries of additional *H. erectus* infant crania.

Mojokerto consists of the majority of the skull cap, including the left side of the frontal torus. The largest missing portions of the skull are from the lateral and inferior occipital regions, the inferior parietals, the squamous part of the temporal, and the right frontal torus (Balzeau et al., 2005). The inside of the skull is packed full of sediment, making it necessary to estimate endocranial volume through digital reconstruction. Using CT scans, Coqueugniot et al. (2004) estimated a cranial capacity of 663 cm³. A second more recent study examining the internal structure of the Mojokerto

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calvaria with CT scans used mirror imaging and some reconstruction of the base of the skull to estimate an endocranial volume of $\sim 630 \text{ cm}^3$ at death (range 620–640 cm^3). Coqueugniot et al. (2004) compared the Mojokerto cranial capacity with adult crania from *H. erectus* to determine that this hominin species had achieved 72–84% of its adult brain size by ~ 1 year of age, consistent with a chimpanzee-like pattern of development. Modern humans have a considerably smaller proportion of their adult brain size achieved by ~ 1 year of age (50% according to Coqueugniot et al., 2004), and therefore experience more (both absolutely and relatively) of their brain growth in a more enriched, social environment during their toddler and early childhood years. An ape-like brain ontogeny for Mojokerto would indicate that *H. erectus* experienced less of its brain maturation during the toddler years and therefore this species may not have been capable of acquiring the complex cognitive skills characteristic of humans, such as symbolic language (Coqueugniot et al., 2004). Leigh (2006) countered that *H. erectus* possessed a more human-like growth pattern based on the absolute brain size of Mojokerto falling within the range of modern humans. Hublin and Coqueugniot (2006) responded that the proportional brain size was the crucial variable in understanding brain ontogeny in this extinct human species. While Mojokerto may fall within the low end of the range of variation of modern human infant cranial capacity, adult *H. erectus* are generally outside the modern human range. In this study, we therefore examine the question of *H. erectus* brain ontogeny using proportional brain size. While we appreciate that absolute brain size can also be used (Leigh, 2006), this study aims to retest the ideas of Coqueugniot et al. (2004) and therefore employs the same approach. However, as can be seen in Fig. 1, the proportional brain size of Mojokerto is highly dependent on the adult *H. erectus* chosen as the comparative sample.

In light of more recent analyses of endocranial volume in Mojokerto (Balzeau et al., 2005) and additional adult *H. erectus* cranial data made available in the last decade, we revisit the issue of brain growth in infant *H. erectus*. Using the two CT-based endocranial volumes for Mojokerto (Coqueugniot et al., 2004; Balzeau

et al., 2005) and a 0.5–1.5 year age estimate (Coqueugniot et al., 2004), we retest the hypothesis that the *H. erectus* brain was growing like a chimpanzee, and test the alternative hypothesis that brain growth in *H. erectus* is similar to that found in modern humans. With the taxon *H. erectus* covering such a wide temporal and geographic distribution, we compare the Mojokerto specimen to various groupings of adult *H. erectus* crania with these conditions in mind.

Materials and methods

Endocranial volumes for 25 human infants aged 0.5–1.5 years were obtained from Coqueugniot and Hublin (2012). Adult human endocranial volumes ($n = 308$) came from Lewis et al. (2011). Chimpanzee endocranial volumes were available from Selenka (1899), Oppenheim (1911), Zuckerman (1928), and Neubauer et al. (2012). One infant chimpanzee from Zuckerman (1928) was pathological, and therefore not used in this study. Additionally, use of five chimpanzee infant brain volumes published by Selenka (1899) and Oppenheim (1911) yielded a percentage of adult endocranial volume (72%) inconsistent with values from Coqueugniot et al. (2004) and Neubauer et al. (2012). We suspect differences in measurement techniques explain these results and therefore we do not include these specimens in our analysis. Chimpanzee endocranial volumes of infants ($n = 4$) came from Zuckerman (1928) and Neubauer et al. (2012) only. Chimpanzee adults ($n = 86$) came from Zuckerman (1928), Isler et al. (2008), and Neubauer et al. (2012).

For brain masses, the human sample consisted of 63 infants aged 0.5–1.5 years, and 863 adult brain masses from individuals 7 years old and over obtained from Marchand (1902). Because it has been reported that brain mass decreases with age (Dekaban and Sadowsky, 1978; Herndon et al., 1999), we performed a second analysis including only individuals less than 50 years old. The differences were negligible and therefore throughout we report results derived from the larger, more inclusive, sample. Brain masses

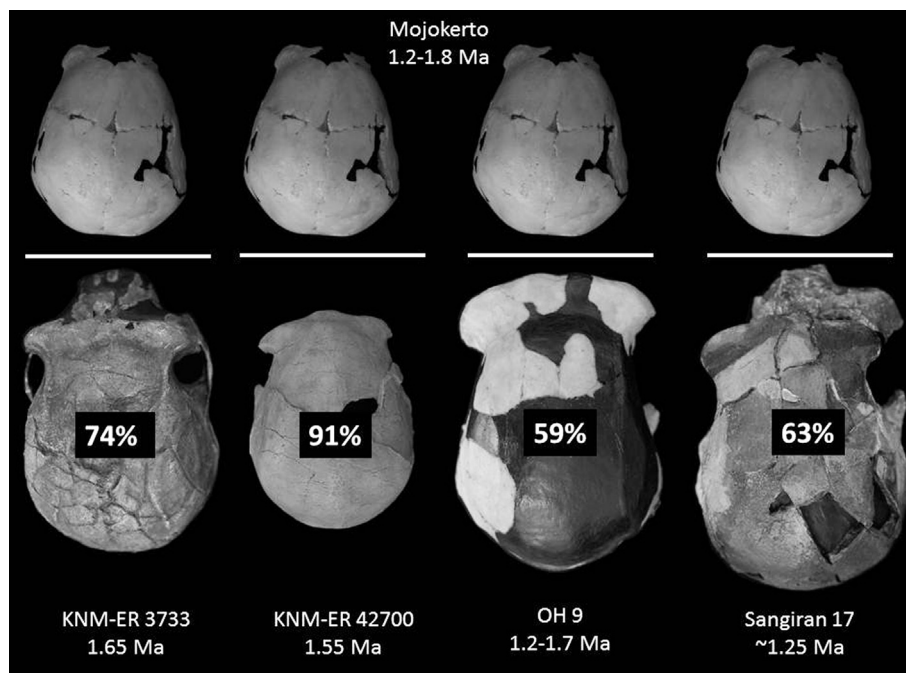


Figure 1. The percentage of adult endocranial volume achieved by Mojokerto when compared with four different adult *Homo erectus* crania. *Homo erectus* is spatiotemporally quite variable, and the choice of a reference sample greatly influences whether the Mojokerto specimen is growing more like a chimpanzee (higher PEV values) or more like a human (lower PEV values).

Table 1
Homo erectus adult crania used in this study.

Specimen	Geological age (Ma)	Location	Date source	EV (cc)	Mojokerto PEV ^a (%)	EV source
D2280	1.77	Dmanisi, Georgia	Rightmire et al., 2006	775	81.3–85.6	Rightmire et al., 2006
D2282	1.77	Dmanisi, Georgia	Rightmire et al., 2006	655	96.2–101.2	Rightmire et al., 2006
D2700	1.77	Dmanisi, Georgia	Rightmire et al., 2006	600	105.0–110.5	Rightmire et al., 2006
D3444	1.77	Dmanisi, Georgia	Lordkipanidze et al., 2006	650	96.9–102.0	Lordkipanidze et al., 2006
KNM-ER 3733	1.65	Kenya	Feibel et al., 1989	848	74.3–78.2	Holloway et al., 2004
KNM-ER 3883	1.57	Kenya	Feibel et al., 1989	804	78.4–82.5	Holloway et al., 2004
KNM-ER 42700	1.55	Kenya	Spoor et al., 2007	691	91.2–96.0	Spoor et al., 2007
KNM-WT 15000	1.53	Kenya	Walker and Leakey, 1993	880	71.6–75.3	Begun and Walker, 1993
OH 9	>1.49	Tanzania	Manega, 1993	1067	59.0–62.1	Holloway et al., 2004
Daka	1.0	Ethiopia	Asfaw et al., 2002	986	63.9–67.2	Gilbert and Asfaw, 2008
Buia	1.0	Eritrea	Abbate et al., 1998	900	70.0–73.7	Machiarelli et al., 2004
Sangiran 2	1.0–1.58	Java	Larick et al., 2001	813	77.5–81.6	Holloway et al., 2004
Sangiran 3	~0.8–1.0	Java	Larick et al., 2001	950	66.3–69.8	Holloway et al., 2004
Sangiran 4	1.58–1.66	Java	Indriati and Antón, 2010	908	69.4–73.0	Holloway et al., 2004
Sangiran 10	1.0–1.58	Java	Larick et al., 2001	855	73.7–77.5	Holloway et al., 2004
Sangiran 12	1.0–1.58	Java	Larick et al., 2001	1059	59.5–62.6	Holloway et al., 2004
Sangiran 17	1.0–1.58	Java	Larick et al., 2001	1004	62.8–66.0	Holloway et al., 2004
Sangiran IX (Tjg-1993.05)	~1.25	Java	Larick et al., 2001	870	72.4–76.2	Kaifu et al., 2011
Bukaran (Sbk-1996.02)	~1.25	Java	Larick et al., 2001	916	68.8–72.4	Grimaud-Hervé et al., 2012
Grogol-Wetan (Gwn-1993.09)	~1.25	Java	Larick et al., 2001	850	74.1–78.0	Grimaud-Hervé, Personal communication
Sangiran 38	1.47–1.58	Java	Indriati and Antón, 2010	850	74.1–78.0	Indriati and Antón, 2010
Trinil 2	~0.8–1.0	Java	Antón, 2003	940	67.0–70.5	Holloway et al., 2004

^a Smaller value based on Balzeau et al. (2005) estimate; larger number based on Coqueugniot et al. (2004) estimate.

of chimpanzees aged 0.5–1.5 years ($n = 12$) and adults ($n = 71$) were provided by Yerkes National Primate Research Center (see DeSilva and Lesnik, 2006). Brain data from mountain gorillas (*Gorilla beringei beringei*; [$n = 6$ infants; $n = 22$ adults] from McFarlin et al., 2013) and sooty mangabeys (*Cercocebus atys*; [$n = 32$ infants; $n = 96$ adults] from Yerkes National Primate Research Center) were also examined to widen the breadth of comparison.

The adult *H. erectus* endocranial volumes ($n = 22$) were collected from sources listed in Table 1. Given that *H. erectus* ranges spatially and temporally, the varied sources of these endocranial volumes allow for a conservative calculation of variation in endocranial volume growth in this species. Proportional endocranial volume was defined as the ratio of Mojokerto's endocranial volume to the adult *H. erectus* endocranial volume, which represents the proportion of brain growth Mojokerto would have achieved by the time of death. We are aware that brain mass and endocranial volumes are not equivalent (Tobias, 1970; Holloway, 1980; Hofman, 1983) and may even yield slightly different ontogenetic patterns (Coqueugniot and Hublin, 2012). We therefore examined both the proportional brain mass (PBM) and proportional endocranial volume (PEV) in humans and chimpanzees.

Statistical analysis

Because *H. erectus* is spatiotemporally widespread, we conducted four separate analyses. The *H. erectus* treatment groups were as follows: A. all *H. erectus* endocranial volumes (EVs) ($n = 22$); B. all but Dmanisi ($n = 18$); C. Indonesian *H. erectus* only ($n = 11$); D. only Indonesian specimens over 1.2 Ma ($n = 9$); Sangiran 3 and Trinil 2 were removed from this last group because they are estimated to be geologically younger than the other Indonesian fossils. Each of these treatment groups were compared to the two Mojokerto endocranial volume estimates: Balzeau et al. (2005) of 630 cm³, and Coqueugniot et al. (2004) of 663 cm³. The proportion of adult endocranial volume (PEV) was determined for Mojokerto by dividing its brain size by the average of the adult *H. erectus* treatment group. We then took the mean proportion of adult brain

size for each of the four treatment conditions, and used that mean (reported in Table 2) as a threshold with which to sort the human and chimpanzee resampled data.

The resampling add-in for Microsoft Excel 2007 was used to generate the statistics. Resampling is a useful method for analysis of hominin fossils, as sample sizes are typically limited. We employed a resampling technique in which one modern human infant brain volume was randomly selected from our dataset and divided by the average of 22 randomly selected human adult brain volumes. This exercise mimics the calculation of the PEV achieved by Mojokerto in which this endocranial volume is divided by the average of all of the adult *H. erectus* specimens. We are unconcerned about mixing human or chimpanzee infants and adults from different populations since the *H. erectus* specimens are derived from different localities and often different time periods. We then repeated the process 10,000 times to develop a distribution of values of proportion of adult brain size achieved by 0.5–1.5 year old humans. The procedure was repeated with chimpanzee brain volumes. We then repeated this entire process using human and chimpanzee brain masses to generate PBM distribution curves. Although we are aware that there may be differences in brain ontogeny between the sexes, the samples were not divided by sex because it is difficult to accurately determine sex in both Mojokerto and in many adult *H. erectus* crania. To avoid the problem of comparing the Mojokerto specimen with a pool of adult *H. erectus* specimens that vary both temporally and geographically, we repeated the procedure using the four treatment conditions already described. We then calculated the frequency at which Mojokerto could be sampled from the

Table 2
Proportional Endocranial Volume (PEV) per *Homo erectus* treatment group.

Treatment	<i>H. erectus</i> EVs used (n)	Mojokerto 630 cm ³ PEV (%) \pm Stdev	Mojokerto 663 cm ³ PEV (%) \pm Stdev
A	All (22)	73 \pm 12	77 \pm 13
B	All but Dmanisi (18)	70 \pm 8	74 \pm 8
C	Indonesia Only (11)	69 \pm 5	73 \pm 6
D	Indonesia >1.0 Ma (9)	70 \pm 6	73 \pm 6

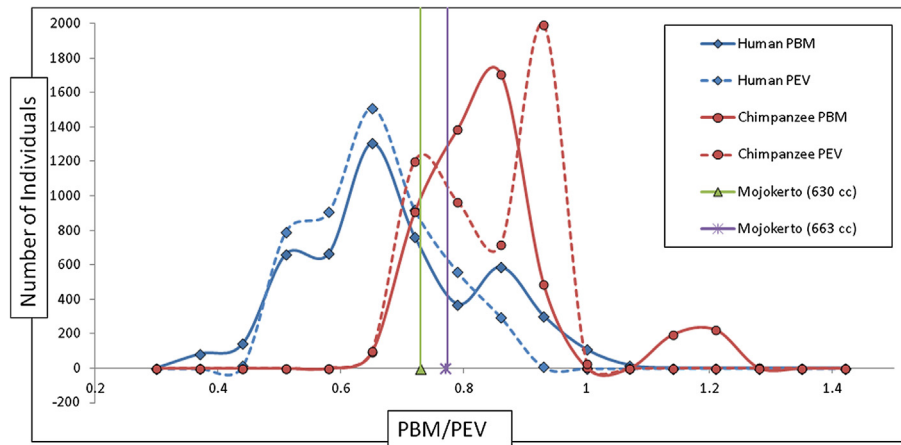


Figure 2. The number of individuals per PEV and PBM is graphed for humans, chimpanzees, and the two brain estimates for Mojokerto relative to all adult *Homo erectus* crania ($n = 22$) greater than ~ 1 million years. Notice that there is considerable overlap between the right tail of the human distribution and the left tail of the chimpanzee distribution. The two Mojokerto estimates fall between the distributions, and could be sampled from either humans or chimpanzees.

human distribution, and how often from the chimpanzee distribution. These data allow us to answer the question, how often is *H. erectus* within the chimpanzee or human brain development range?

Results

Humans achieve an average of 62% ($\pm 10\%$) of their adult endocranial volume by 0.5–1.5 years of age, while chimpanzees have a higher 80% ($\pm 9\%$) of their endocranial volume completed by the same age. Humans achieve 65% ($\pm 14\%$) of their adult brain mass by 0.5–1.5 years old, while chimpanzees have 81% ($\pm 12\%$) by that time. The chimpanzee data are nearly identical to the PEV calculated by Coqueugniot et al. (2004) though our human data yield higher values. There is consistency in chimpanzee brain ontogeny whether PEV or PBM is used. Human PEV and PBM are not as concordant, which is consistent with findings of Coqueugniot and Hublin (2012).

To test the assumption that the chimpanzee is a good representation of ape brain ontogeny in general, we also examined mountain gorilla brain masses of adults and 0.5–1.5 year olds (McFarlin et al., 2013). Using the same resampling methods that

were used for humans and chimpanzees, mountain gorillas achieve 78% ($\pm 16\%$) of their brain growth by this age. *Cercocebus* monkeys have achieved a higher 83.4% of their adult brain mass by this time. Gorillas are similar to chimpanzees in this respect, and both apes were smaller than the monkey average.

Using Balzeau et al.'s (2005) estimate of 630 cm³, Mojokerto had achieved between 69 and 73% of its adult endocranial volume at the time of its death (Table 2). If Coqueugniot et al.'s (2004) estimate of 663 cm³ is used, Mojokerto had achieved between 73 and 77% of its adult endocranial volume, consistent with what was previously reported (Coqueugniot et al., 2004). Based on the most recent endocranial volume estimate and perhaps most relevant *H. erectus* adults (those from Indonesia that are >1.2 Ma), Mojokerto had achieved 69–73% of its adult cranial capacity at the time of its death. These results indicate that the adult reference sample can impact PEV calculations.

As shown in Figs. 2 and 3, Mojokerto's PEV falls within both the human and chimpanzee distributions, regardless of the different adult crania treatments employed and regardless of whether PEV or PBM is the comparative metric. Table 3 displays the p -values indicating the likelihood of sampling the PEV or PBM reached by the Mojokerto calvaria from either the human or chimpanzee

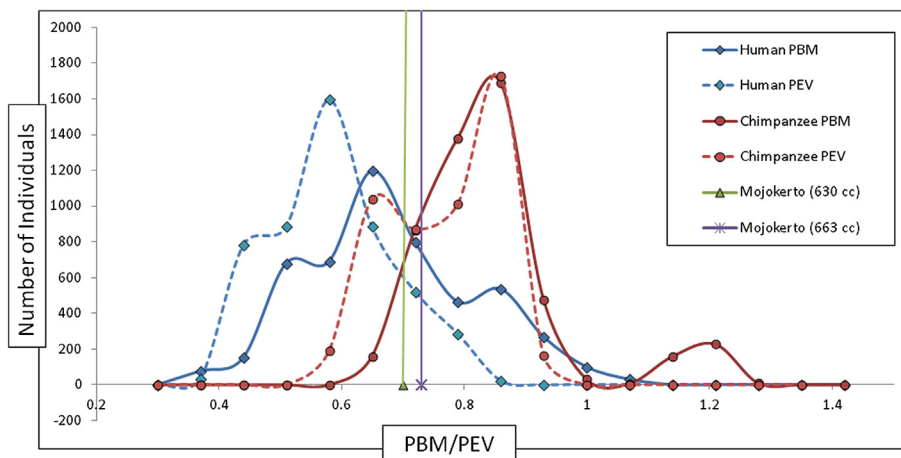


Figure 3. The number of individuals per PEV and PBM is graphed for humans, chimpanzees, and the two brain estimates for Mojokerto relative to all adult *Homo erectus* crania from Indonesia greater than 1.2 million years ($n = 9$). Notice that there is considerable overlap between the right tail of the human distribution and the left tail of the chimpanzee distribution. The two Mojokerto estimates fall between the distributions, and could be sampled from either humans or chimpanzees.

Table 3

P-values representing the chance of sampling an infant with a PEV or PBM of Mojokerto from the human sample and from the chimpanzee sample.

Treatment	<i>H. erectus</i> used	Human (H), chimpanzee (C)	PEV		PBM	
			P (630 cm ³)	P (663 cm ³)	P (630 cm ³)	P (663 cm ³)
A	All	H	0.16	0.09	0.26	0.22
		C	0.25	0.34	0.24	0.39
B	All but Dmanisi	H	0.21	0.13	0.31	0.26
		C	0.24	0.26	0.15	0.25
C	All Indonesia	H	0.22	0.15	0.34	0.27
		C	0.21	0.25	0.13	0.23
D	All Indonesia >1.2 mya	H	0.20	0.15	0.32	0.26
		C	0.22	0.25	0.14	0.26

distributions for each treatment and using both endocranial volume estimates. These were determined in the following manner. The number of values of PEV or PBM reached by 0.5–1.5 year olds that were greater than the Mojokerto value was calculated from the human distribution to test if the hypothesis that *H. erectus* brain development was statistically distinct from that of modern humans could be refuted. Similarly, the number of PEV or PBM values reached by 0.5–1.5 year olds that were less than the Mojokerto value was calculated from the chimpanzee distribution to test if the hypothesis that *H. erectus* brain development was statistically distinct from that of modern chimpanzees could be refuted. For instance, in treatment A with 630 cm³ endocranial volume and PBM as the comparative metric, we obtained the following results: ($p = 0.26$) for humans and ($p = 0.24$) for chimpanzees. This means that 26% of resampled modern human values were more ape-like than Mojokerto is, and 24% of resampled chimpanzee values were more human-like than Mojokerto is. Of note, when PBM is the metric the Mojokerto specimen has a more human-like developmental trajectory. When PEV is the comparative metric, the chimpanzee pattern has higher p -values. However, in no case, using either metric, can we refute the hypotheses (at a $p = 0.05$ level) that Mojokerto developed like a human or a chimpanzee.

Discussion

Having achieved roughly 70% of its full brain size by 0.5–1.5 years of age, Mojokerto falls between the value for chimpanzees (80%) and humans (62%) of the same chronological age. Only if all *H. erectus* crania and the Coqueugniot et al. (2004) endocranial volume are used do we find an ape-like developmental trajectory for Mojokerto, but even this fails to reach statistical significance ($p = 0.09$). If one is more selective, and arguably more accurate, in utilizing only the Indonesian *H. erectus* over 1.2 Ma, the percentage of adult brain size achieved by Mojokerto is no more likely to be sampled from a chimpanzee distribution than a human one, though neither reaches statistical significance (Table 3). Our methods artificially inflate the amount of variation, and therefore, overlap, between human and chimpanzee PEV and PBM. We regard this as a conservative approach and the most appropriate until longitudinal data on brain ontogeny in humans and chimpanzees are available. The fact that the average *H. erectus* PEV (70%) falls almost exactly between the average human (62%) and chimpanzee (80%) PEV suggests an intermediate brain ontogeny in this hominin species whether cross sectional data (which would increase variation) or longitudinal data (which would decrease variation) are used.

We therefore cannot refute the hypothesis that *H. erectus* brains were growing like a human or the hypothesis that they were growing like a chimpanzee. Instead, Mojokerto's brain development falls within the range of both no matter which brain metric is used, and no matter which grouping of *H. erectus* adults are used. We therefore suggest that the dichotomization of brain development, and perhaps many other life history variables, as either 'human-like' or 'ape-like'

is the wrong approach. *H. erectus* brain development was not exclusively chimpanzee-like; it was not exclusively human-like. It was *H. erectus*-like. *H. erectus* was likely developing uniquely, along the continuum of variation between the human and chimpanzee distribution. Of course, this point assumes that chimpanzees are representative of the brain development pattern of the last common ancestor, the validity of which is currently unknown. However, given the PBM results reported in this study for mountain gorillas, and given that the late Miocene hominids have brains on the small end of the chimpanzee size range (Kordos and Begun, 2001; Zollikofer et al., 2005; Suwa et al., 2009), we regard this assumption as reasonable.

This finding is consistent with previous suggestions that *H. erectus* displayed a developmental trajectory between modern humans and apes. DeSilva and Lesnik (2008) suggested that the proportion of adult brain size achieved at birth in *H. erectus* falls in between that of chimpanzees and modern humans, though closer to the modern human range. Dean and Lucas (2009) reviewed findings based on the Nariokotome skeleton (KNM-WT 15000) and concluded that *H. erectus* had a skeletal growth trajectory that was intermediate between those of humans and apes (though Dean and Smith (2009) presented dental evidence for more of an ape-like pattern of growth). The placement of the neonatal line (NL) (Zanolli et al., 2011) on two Javanese *H. erectus* deciduous teeth closely resembled that of extant humans (Zanolli et al., 2012), supporting the idea of a more human-like pattern of developmental timing. From these results, we see that *H. erectus* is in some ways developmentally transitional between a modern chimpanzee and modern human, and it remains possible that there may be some decoupling of dental, skeletal, and brain growth ontogenies in these early hominins.

While we suggest that *H. erectus* brain development was unique, the data presented here suggest that this hominin may have already been transitioning away from the rapid brain ontogeny characteristic of modern apes. What might the developmental pattern look like in a *H. erectus*? Delayed brain development most likely would have had important behavioral and cognitive implications for *H. erectus*. Schoenemann (2012), for example, has argued that larger brains, such as those possessed by *H. erectus*, have implications for behavior, including an increased reliance on learning during development. Perhaps an individual like the Mojokerto child would have had an initial period of brain development slightly accelerated relative to modern humans, but slower than that of modern apes, thus experiencing more of its brain development and more potential for learning during its toddler years. Dunbar (1996) has suggested that, with their larger-than-ape brains, more complex vocal communication would also have been important for *H. erectus*. Given that the evolution of language, as we know it today, would probably have taken time to evolve, the foundations of language may have already been present in *H. erectus*, and acquisition of language may benefit from slower brain development during those toddler years. As Nowell (2010) points out, one of the most important changes to brain structure

over the course of human evolution (that of the frontal lobe and areas responsible for functions involved in 'working memory') had already taken place in fossils attributed to early *Homo* by 1.5–2.0 Ma (Holloway et al., 2004).

However, we caution that behavioral reconstructions based on brain ontogeny alone are speculative, and particularly so given that brain growth in *H. erectus* can only be inferred from a single infant (Mojokerto). Thus, as with any issue of reconstructing our evolutionary past, finding more fossils, in this case of infants and juveniles, will be the best way to continue to refine our understanding of development in *H. erectus* and to shed more light on the evolution of human patterns of brain ontogeny.

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